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Impact of the Western Spruce Budworm on Buds, Developing Cones and Seeds of Douglas-Fir in the Intermountain Region

Charles Joseph Frank
Utah State University

IMPACT OF THE WESTERN SPRUCE BUDWORM ON BUDS, DEVELOPING CONES AND SEEDS OF DOUGLAS-FIR IN THE INTERMOUNTAIN REGION

by

Charles Joseph Frank

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Charles J. Frank

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ABSTRACT

Impact of the Western Spruce Budworm on Buds, Developing Cones and Seeds of Douglas-fir in the Intermountain Region

by

Charles J. Frank, Master of Science

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Major Professor: Dr. Michael J. Jenkins
Department: Forest Resources

The western spruce budworm, Choristoneura occidentalis Freeman (Lepidoptera: Tortricidae), is a serious defoliator of conifers in the western U.S. and western Canada. In 1985 epidemic levels of the budworm caused average tree defoliation in west-central Idaho to increase to 83%, up substantially from the 35% average tree defoliation of 1984. Associated with this increase in defoliation was a change in the relative stand defolation ranking between the two years. In 1985 the budworm was found to damage all types and developmental stages of reproductive structures of Douglas- fir, including: seed-cone buds, pollen-cones buds, maturing cones, and seeds. Differential selection of feeding sites was observed, with a significantly higher proportion of larvae found in seed-cone buds than in pollen-cone buds. Shortly after larval

emergence, 25% of the total number of seed-cones buds were infested. A subsample of 171 branch tips indicated that only 9% of pollen-cones, while less than 2% of the vegetative buds contained larvae. A total of 640 cones from 21 trees were examined. Of these cones, 76% were infested with larvae, however not all of the seeds were destroyed. The average percent of destroyed seeds per tree was found to be exponentially related to the average current defoliation of the tree.

(63 pages)

REVIEW OF THE LITERATURE

The purpose of this section is to acquaint the reader with existing literature regarding the western spruce budworm, Choristoneura occidentalis Freeman, (Lepidoptera: Tortricidae). Several topics are discussed, including the biology and ecology of the insect, damage caused by the insect, sampling methods, and finally control measures. The topics that deal specifically with the objectives of the project are given more intensive coverage, for example impact to seed production and sampling techniques developed to assess this damage. Other topics, such as chemical control, are beyond the scope of this paper and are only briefly discussed. The majority of the information is relatively recent, a direct result of an international cooperative project organized in 1977 between the U.S. and Canada, known as the CANUSA project. McKnight (1968a) compiled an exhaustive review of the literature on the subject up through that time. The reader is referred to that work to supplement what is presented here.

Biology and Ecology of the Western Spruce Budworm

The western spruce budworm, Choristoneura occidentalis Freeman, is the most widely distributed and destructive defoliator in western coniferous forests (Carolin and Honing, 1972). It is closely related to its eastern counterpart, the spruce budworm, C. fumiferana (Clemens).

Not until 1967 were the two species considered distinct from each other. Freeman (1967) described the morphological characteristics used in differentiating the two species. Nearly a dozen species of Choristoneura are listed and described by Furniss and Carolin (1977) as being serious defoliators of conifers in North America. Stevens et al. (1984), and Carolin and Stevens (1979) prepared taxonomic keys for identification of other Choristoneura species as well as other lepidopterans associated with the western spruce budworm.

Because the western spruce budworm and the spruce budworm are serious economic pests the long term CANUSA project has resulted in more research being conducted for these two insect pests than for any other forest pest in North America (Knight and Heikkenen, 1980).

Hosts

Both the spruce budworm and the western spruce budworm feed primarily on conifers. The preferred hosts of the former are white spruce, Picea glauca (Moench) Voss, and balsam fir, Abies balsamea (L.) Mill. The latter prefers Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, grand fir, Abies grandis (Dougl.) Lindl., subalpine fir, A. lasiocarpa (Hook.) Nutt., Engelmann spruce, Picea engelmannii Parry, and western larch, Larix occidentalis Nutt. Other conifers that occur in the range of the western spruce budworm can serve as occasional hosts. Douglas-fir,

because of its relatively high economic value, is the emphasis of this report.

Life Cycle

Fellin et al. (1983), Fellin and Dewey (1982), and Carolin and Honing (1972) described the one year life cycle of the western spruce budworm. Moths emerge in July or August and after mating the female will normally deposit some eggs prior to leaving the stand. Greenbank (1973) found, however, that females developing from starved larvae can fly before ovipositing, and that the proportion increases with increasing larval starvation. This may not always be the case as Morris (1955) found high egg mass counts on severely defoliated trees. Harris and Dawson (1982) analyzed egg masses and found a range of 2 to 105 eggs per egg mass (mean 35), a slightly higher mean of 48 eggs per egg mass was found by Campbell et al. (1984). It was also found that the eggs were laid in rows ranging from 1 to 4 rows per egg mass with the vast majority being laid in three rows.

Egg eclosion occurs about 10 days after they are laid. The emerging larvae then seek shelter in lichens, bark crevices and under bark scales where they spin a hibernaculum and overwinter. The distribution of hibernating larvae on Douglas-fir was investigated by McKnight (1969). He found 65% of the hibernating larvae on branches and 35% on the bole. About 27% hibernate on the

branches in the lower one-third of the crown. Carolin and Coulter (1972) found that 79% of all hibernating larvae were on the limbs in the mid-crown. An alternative overwintering site for the spruce budworm (the mined staminate buds of balsam fir) was discovered by Batzer (1960) and Blais (1952). Regardless of where the larvae hibernate it was determined by Morris et al. (1958) that they usually do so within several hours after eclosion.

Around May the larvae emerge as second-instars and begin wandering in search of food. Thomson (1979) noted that the second-instar larvae are photopositive and move to the terminal portion of twigs where they begin mining old needles or expanding buds if any are available. Several weeks after larval emergence the vegetative buds begin to swell followed by the flushing of the new shoots. The larvae then turn their attention to the new foliage and continue feeding until pupation. During this period of feeding the larvae can, under severe conditions, consume 100% of the new foliage and may even feed on the previous season's foliage. Of all the damage caused by the feeding larvae, it was estimated by Miller (1977) that 87% of the total amount of food consumed was done by the sixth-instar larvae, the last larval stage before pupation. Besides feeding on foliage the larvae also feed on reproductive buds, small conelets and the maturing cones. After 30 to 40 days the larvae pupate and remain in this stage for about

10 days before emerging as adults to complete the cycle.

Phenology

Virtually all conifers in the western U.S. are vulnerable to the western spruce budworm with the preferred host being grand fir and Douglas-fir. The life cycle of the western spruce budworm closely coincides with the phenology of its hosts. As mentioned, the larvae emerge in the spring prior to bud burst and begin feeding on old needles until new needles become available. The new foliage normally becomes available 2 to 3 weeks after the larvae emerge, but this period can vary considerably depending on the weather. If conditions are such that the larvae emerges significantly earlier than bud burst heavy mortality can result (Morris et al. 1958). This mortality can be attributed to either starvation or to dispersal losses. Thomson et al. (1984) determined that in an area they studied the optimal time between larval emergence and bud flush was around 17 to 18 days. Any deviation from this optimum would result in greater larval mortality. Bud flushing, larval emergence, and other phenological events can partially be determined by degree days.

Degree days are calculated using three parameters: a critical temperature threshold, a starting date, and total heat units. Using an iterative technique, Thomson and Moncrieff (1982) determined that average bud flush of Douglas-fir could be accurately predicted using a threshold

temperature of 2.78°C beginning March 12th and accumulating 578 heat units. Other temperature thresholds have been suggested for predicting larval emergence and bud flushing. Bean (1961) used a threshold temperature of 2.5°C for spruce budworm in Minnesota. In developing insect and host tree phenology models, Beckwith and Kemp (1984) used a threshold temperature of 5.5°C. Volney et al. (1983), however, found that for the budworm population they studied in Oregon the threshold temperature was significantly higher than 5.6°C. Arnold (1960) explained how to compute heat units using maximum and minimum temperatures, and Allen (1976) described a computer technique for determining degree days using a modified sine wave method.

The more closely synchronized larval emergence is to bud flush, the greater the subsequent damage can be to the host. Kemp (1984) looked at defoliation levels for a two year period and compared it to the phenology of the host for each of those years. In 1982 defoliation was light to moderate followed by heavy defoliation in 1983. In 1982 shoot elongation at the peak of the population of third-instar larvae was only 2% complete as compared to 23% in 1983. The increase in the level of defoliation between the two years was explained as being related to the relative success the larvae experienced in finding food.

Variations in the phenology of Douglas-fir can partially be explained by genetic variability (Wulf 1982) and other environmental conditions. As a corollary to the

findings of Cleary and Waring (1969), Kemp and Beckwith (1984) suggested the persistence of a snow pack may keep the soil cold, thereby delaying budburst.

Damage

The first recorded outbreak of the western spruce budworm in North America was in Vancouver, B.C. in 1909. In 1922 two large outbreaks occurred in Idaho followed in 1949 by a large outbreak in the northern Rocky Mountains. The latter outbreak still persists today (Fellin and Dewey 1982). Kucera and Taylor (1985) reported that 4.8 million ha. experienced defoliation in western North America and western Canada in 1983. In 1984 the figure had dropped to 4.5 million ha. with some states and Canadian provinces reporting increases while others reported a decline in defoliation level.

The western spruce budworm feeds primarily on foliage, consequently most of the damage can be attributed directly or indirectly to defoliation. The budworm also feeds on reproductive structures including buds, conelets, and maturing cones resulting in the reduction of potential seed production.

Defoliation Induced Damage

The preferred food of the budworm is the current year's foliage of the host tree. The larvae will feed on older foliage early in the season prior to vegetative bud

flushing and again later in the season if heavy defoliation has resulted in the consumption of all new foliage, a habit known as back feeding. Removal of the current year's foliage, especially if continued over a number of years, can result in a reduction of radial and height increment, top-killing, and even mortality. Also associated with successive years of defoliation is the predisposition of weakened trees to secondary insects and pathogens, and a change in the competitive status of an individual tree or species. In addition, larvae occasionally cause physical damage to the new shoots of some host species (Fellin and Schmidt 1967).

Radial increment is reduced if defoliation is severe enough to remove most of the new foliage. The amount of reduction varies between tree species and tends to lag defoliation by one year. Williams (1966) looked at the radial increment loss in grand fir, Engelmann spruce, and Douglas-fir. Grand fir suffered the greatest loss with the amount of loss being related to the defoliation intensity. Douglas-fir experienced the least reduction and Engelmann spruce was somewhere in between. Differential reduction in radial increment was also reported by Brubaker and Greene (1979). They found that the 5-year growth loss of grand fir was 20 times that of Douglas-fir. Alfaro et al. (1982) combined the effects of 4 different outbreaks and calculated an average reduction in diameter of 5.5 cm equating to a 12% reduction in increment. Another important

result of severe defoliation is a reduction in height growth. Van Sickle et al. (1983) attributed height growth loss to 3 factors: (1) reduced height growth during the outbreak; (2) reduced height growth during recovery; and (3) dieback of the main stem. These factors can affect any host species, but again grand fir seems to be most susceptible, especially to dieback. Williams (1966) assigned trees to damage classes of 1 to 4 based on amount of defoliation, ranging from very little (1) to severe (4). There was no dieback (top-killing) of the grand fir in damage class 1. In the other 3 classes, however, 65%, 91%, and 92% of the trees, respectively, experienced top-killing.

The result of reduction in radial and height increment is the corresponding reduction in volume. Volume loss can be determined as explained by Thomson and Van Sickle (1980). A computer model is used to estimate potential growth. Volume loss is then calculated as the difference between the potential growth and the actual growth. Using this method, Alfaro et al. (1985) estimated a volume loss of 60 cubic meters/hectare for a 5-year outbreak.

Tree mortality caused by the feeding of the western spruce budworm also varies with species, as well as with the severity and duration of an outbreak. Incidental mortality can also occur, a result of weakened trees being predisposed to other insects and pathogens.

Silver (1960) investigated an outbreak in British

Columbia that began in 1953, increased to a major epidemic the following year and collapsed in 1959. During the outbreak no Douglas-fir died, even though 90% of the needles were lost and bud damage was heavy. Alfaro et al. (1982), however, studied a 5-year outbreak and found contrasting results. They recorded an unusually high mortality rate of almost 40% of the trees in the sample plots. This figure was reduced to about 25% when the suppressed trees, assumed to die anyway, were excluded. They determined that before any mortality occurred a tree had to experience a cumulative defoliation greater than 175% over the course of the outbreak. Mortality increased to 80% among trees with greater than 350% cumulative defoliation. Trees severely defoliated by the budworm may not die as a direct result of the defoliation but because of reduced vigor may become more susceptible to other destructive agents.

Alfaro et al. (1982) noted the immigration of the Douglas-fir beetle, Dendroctonus pseudotsugae Hopkins, into a stand one year after defoliation by the budworm declined. The following year 17% of the sample trees were infested by the beetle, though most recovered within several years. Of the total number of trees that died during or shortly after the budworm outbreak, only 2% were attributed to the activity of the beetle. Trees that are weakened or top-killed by the budworm can also be attacked by fungal pathogens. Such a pathogen is the Indian paint fungus,

Echinodontium tinctorium Ell. and Ev., (Ferrell and Scharpf 1982).

A common effect of defoliation in mixed stands is a change in the competitive status of an individual or a species. This happens when several neighboring trees exhibit differential damage as a result of defoliation. Williams (1966) showed that under similar conditions grand fir grows faster than Douglas-fir and can easily over-top it. During a budworm outbreak, however, grand fir typically receives a disproportionately greater amount of defoliation than adjacent Douglas-fir, and in addition, often experiences top-killing. Because Douglas-fir receives less damage and is quick to recover following an outbreak, the overall effect is to allow it to assume a dominant position.

Fellin and Schmidt (1967) observed that in western Montana the western spruce budworm is responsible for severing the stems of terminal and lateral shoots of western larch. They stated that some stems are only scored or superficially mined, but usually a large section is chewed out of the stem. This damage, they concluded, does not seem to be related to defoliation level. Kulman and Hodson (1961) reported similar damage to jack pine P. banksiana Lamb. by the jack pine budworm C. pinus Freeman. Tip mining also occurs in lodgepole pine P. contorta Dougl. by C. lambertiana (Busck.), but the preferred food for these larvae are staminate flowers and cones.

A high degree of variability in defoliation may exist within and between trees. McDonald (1981) investigated this variability and presented a number of hypotheses to address it. These hypotheses included escape, microsite differences, larval feeding preferences, predator and parasite effectiveness, and phenologic asynchrony of the insect and host. Redak and Cates (1984) looked intensively at the chemical composition of the foliage (foliage quality) and demonstrated that differential defoliation of trees can partially be explained by the chemistry of the foliage. Using budworm larval dry weight as the dependent variable they showed that the most important independent variable was foliage quality. Much less important were tree physical and phenotypic factors.

Variation in intratree defoliation is primarily a result of budworm behavior and foliage distribution within the crown. This variability is most pronounced during low and moderate larval populations (Chrisman et al. 1983). Larvae will usually feed on one shoot until all of the new foliage has been consumed before moving on to another shoot. The result of this behavior is that some shoots will be completely defoliated while others are untouched, causing a great amount of variability. Conversely, during years of high larval populations the majority of the shoots will receive heavy defoliation, effectively reducing the variability.

Cone Damage

Reduced cone and seed production can be a serious consequence of budworm activity. This impact results from defoliation and bud killing, and from the larvae feeding on the reproductive structures.

Although hard to quantify, it has been shown that defoliation can affect the subsequent cone production by reducing shoot length, thereby reducing the number of sites upon which reproductive buds could develop, and by affecting the proportion of buds taking the different pathways described by Owens (1976). Krueger (1967) demonstrated that minerals and carbohydrates stored in one-year old shoots of red pine Pinus resinosa Ait. contributed substantially to the expanding shoots. In a similar study Kozlowski and Winget (1964) determined that old needles contributed about four-fifths or more to the total shoot length, with the majority coming from the stored carbohydrates in the one-year old needles. Schooley (1978) looked at the effect of severe defoliation on the number and size of shoots of balsam fir. Chrisman et al. (1983) found that in most cases cone production is highest in lightly defoliated stands. They pointed out that defoliation not only reduces the photosynthetic capacity needed for reproductive bud development, but that it also provides unfavorable conditions for bud initiation resulting in more vegetative or aborted buds.

More apparent than the effect of defoliation on cone

production is the loss from direct feeding damage to reproductive buds, conelets, and maturing cones.

This direct damage to potential seed production begins before bud burst and continues until the larvae pupate. About the time of larval emergence in the spring the reproductive buds are beginning to expand, making them particularly vulnerable to the hungry larvae. As the female buds burst small conelets are formed, and it is at this stage that the most serious impact to the cone crop can occur. Fellin et al. (1983) estimated that 30% of the potential cone crop can be destroyed by the third week of May, and 100% by early June when larval populations are high and the cone crop is light. Schooley (1978) found that although the spruce budworm did not destroy the buds of balsam fir, they destroyed many cones in the "flower" stage (conelets). Fellin and Dewey (1982) explained that the damage caused by a single larva is increased because rather than confine their feeding to a single cone the larvae move around and attack numerous cones.

In Douglas-fir much of the cone damage is caused by larval tunneling in the cone, possibly in preparing a site for pupation. The proportion of seeds destroyed by tunneling versus the number destroyed by actual consumption has not been determined. Fellin and Shearer (1968) showed that the western spruce budworm is responsible for cone damage to western larch. They found that damage to larch cones was variable, with some cones being slightly scored

and others being severely damaged. Damage to cones by other budworm species has been reported. Stark et al. (1965) estimated that 90% of the female cones of lodgepole pine were infested by C. lambertiana (Busck.), and damage to one-year old cones of jackpine by C. pinus Freeman was reported by Kulman et al. (1963).

Sampling

Douglas-fir is a species of relatively high economic value thus much research has gone into evaluating damage caused by the western spruce budworm. Most of the damage is a direct result of defoliation, which in turn is dependent upon the population levels of the budworm (Carolin and Coulter 1972). By determining these two parameters, population levels and defoliation, correlations can be made between the number of larvae and the potential damage. To determine populations, either absolute or relative, many techniques have been developed for measuring egg masses, larvae, pupae, and adult populations, as well as for measuring dispersal of larvae which could affect local populations. Several techniques are used to determine defoliation with the most commonly used being ocular estimates and shoot-count methods.

A comprehensive plan was developed by Morris (1955) for sampling spruce budworm populations. This plan is the basis for essentially all of the sampling techniques

developed since that time and is used, at least in part, by the majority of researchers working with budworm and other defoliators. Although developed for the spruce budworm, Carolin and Coulter (1972) modified the work of Morris to develop a sampling scheme specific to the western spruce budworm.

The sampling unit used when studying populations is an entire branch or a branch tip, with a "correction factor" applied to convert to an area of foliage. This correction factor, as explained by Morris (1955), is an estimate obtained from the length and width at mid-length of the sample unit. An improvement of the correction factor can be made by assigning a triangular or rectangular form to each sample unit as done by Schmid and Farrar (1982). The length and width measurements are then used to compute the surface area of the geometric form. In determining defoliation, however, conversion to a per area of foliage is not necessary.

Population and defoliation estimates are usually made for each of 3 or 4 crown levels and then extrapolated to the entire tree. It is important to remember that because each level varies in amount of foliage, a weight proportional to foliage amount must be applied to each level. For trees with crowns reduced by crowding, Carolin and Coulter (1975) used three crown levels and applied weights of 1 for the upper one-third, 3 for the middle one-third, and 5 for the lower one-third. Schmid and Morton

(1981) suggested that different weights of 1:3.5:2, respectively, be used for open-grown trees.

When determining population levels any stage of the life cycle of the insect can be sampled. Egg masses, hibernating larvae, feeding larvae, pupae, or adults can be sampled depending on the objectives. The latter two stages are seldom sampled, however, because they can easily be measured indirectly from other stages such as egg masses. A crucial element of sampling any of these stages is the timing of the sampling. Carolin and Coulter (1972) stressed the importance of timing, emphasizing that sampling should not be conducted when larvae are changing their distribution, i.e. from hibernaculum to old needles or expanding buds, or when changes are occurring in stages of the life cycle. Stages of relative stability include egg masses, hibernating larvae, and larvae in expanding buds. The optimal timing of sampling can best be determined from a life table such as developed by McKnight (1971).

Egg masses are frequently sampled to provide an estimate of potential initial density. When sampling egg masses, Twardus and Carolin (1984) pointed out the importance of correctly differentiating between old and new egg masses. The sample unit for egg mass surveys, as well as other population parameters, is the branch tip. The size and number of branch tips vary. Stipe et al. (1977) used two 70 cm. branches from opposite side of the mid crown while Campbell et al. (1984) used a "tip set" comprised of

three 45cm branch tips, a terminal and two side lateral tips. McKnight (1968b) found a 24 inch branch tip to be an adequate size for sampling egg masses. After determining the number of egg masses per square-meter of foliage surface area, Jennings et al. (1983) explained the conversion to absolute number per hectare.

Terrell (1959) described a method for sampling over-wintering larvae. Billets (bole segments) and sections of limbs are cut and placed in emergence containers in a warm location. The emerging larvae are then drawn by light into an attached collection vial and counted. This technique is similar to that described by McKnight (1969).

There are two periods in the life cycle of the budworm during which time the larvae are dispersing: (1) immediately after eclosion, when the first-instars are actively seeking an over-wintering site, and (2) after spring emergence when the second-instar larvae begin searching for food. Regniere and Fletcher (1983) found that the first-instars normally disperse within the crown, while the second-instars disperse more freely between crowns. Sampling during the first period will estimate the number of larvae potentially available to cause damage in the following season. A subsequent survey after spring emergence will yield an estimate of over-wintering mortality and a more accurate estimate of the larval population. A good presentation of sampling design, as well as directions for building four different ground deployed

traps for measuring early larval dispersal is illustrated by Jennings et al. (1984). Beckwith and Burnell (1982) devised a trapping system that measured the number of larvae reaching the forest floor and the dispersal of larvae at different levels above the ground.

The determination of budworm populations is important because it provides an estimate of the number of larvae available to feed upon the host. Knowing the amount of defoliation that can be expected for any given larval population can aid in estimating the potential damage to a tree. Correlation and prediction models can be developed to accurately determine damage once the independent variable, defoliation, has been estimated. The two most frequently used techniques for determining defoliation are ocular estimates and shoot-count methods.

Ocular estimates are usually made from the ground using binoculars. Carolin and Coulter (1975) use this technique for obtaining defoliation estimates by crown levels and then apply a weighting factor to each level to determine the percent defoliation for the entire tree. The advantage of this method is that it eliminates the need to climb trees, thus reducing sampling time, but it is not as accurate as shoot-count methods and depends upon the ability of the observer to be able to estimate consistently from level to level and from tree to tree. A more accurate means of determining defoliation is the shoot-count method. A commonly used shoot-count method is referred to as the

Fettes' method, named for the originator of the technique. Allen et al. (1984) described the use of this method in determining the effectiveness of an insecticide application. To use this method a number of current year's shoots from several branch tips are collected and a visual estimate of missing needles made. Each shoot is then assigned to one of 12 categories based on percent defoliation. The percent defoliation per branch is then determined by averaging the midpoint of each category. Once defoliation per branch is determined the average defoliation per level is computed and finally defoliation for the entire tree is calculated as in the ocular estimate. The drawback of this method is that it is considerably more time consuming than an ocular estimate because of the need to collect a number of branch tips. Normally the branch tips are collected from the ground using pole pruners, but large trees generally require climbing.

MacLean and Lidstone (1982) evaluated these two methods and found the results to be quite similar. They found the shoot-count method to be the most accurate, but that accuracy decreased as defoliation decreased. The accuracy of the ocular estimate was found to be about 5 to 10 percent less than that of the shoot-count method and was dependent upon the degree of previous years defoliation. At low levels of current year defoliation the ocular method tended to over-estimate defoliation. A primary factor

influencing accuracy of the ocular estimate was the experience of the observer. Experienced observers could usually estimate defoliation 5 to 10 percent closer to the true defoliation than an inexperienced observer. Because the shoot-count method produces more accurate estimates is not enough reason to completely dismiss the ocular method. Considerations such as cost of sampling and the required degree of accuracy should dictate the choice of method to use for determining defoliation.

By understanding the population dynamics of the western spruce budworm, and the damage that it is capable of causing, it is possible to produce mathematical and computer models that can help predict budworm populations and consequential damage. Carolin and Coulter (1972), for instance, developed regression models that can predict the number of larvae from the number of egg masses, the number of feeding larvae from the number of hibernating larvae, the number of larvae from the number of pupae, the amount of damage from the number of egg masses, and the amount of damage from the number of larvae. A budworm computer model is presently being developed that links to PROGNOSIS (Stage, 1973), a timber growth and yield model, and will have the ability to predict the reduction in tree and stand volume at different levels of budworm infestation.

Management

Chemical Control

Treating budworm infested areas with chemicals to reduce defoliation began in 1927 with the use of calcium arsenate. This was a one-time application which was not followed by other chemical treatments until DDT was made available in the early 1940's. Large dosages of DDT were used resulting in high mortality of budworm larvae. This chemical was also responsible for destroying non-target insects, birds, mammals, and even fish. Because of its indiscriminate nature and accumulative effects, DDT was banned in 1973. Other pesticides have since been developed and are being used to control the spruce budworm. Shea and Nigam (1984), and Montgomery et al. (1984) discussed chemicals presently registered for use in the U.S. and in Canada for spruce budworm control. Also discussed is the timing of application and the design of an aerial spraying program. Stipe et al. (1977) detailed a project in which Orthene was sprayed to control the western spruce budworm in Idaho. The project resulted in a 91 percent reduction of the budworm population at a cost of $9.60 per acre.

Chemicals are also being used to protect individual trees from budworm damage. These efforts are costly and are usually directed towards decreasing cone and seed damage. Two techniques are being used to treat individual trees; ground spraying, and chemical implantation and

injection.

Stipe (1984) described the application of acephate and carbaryl to individual trees. They reported a seed yield increase of 50 percent with this type of treatment if applied at the proper time. Two applications were used, with the first being timed with spring larval dispersal followed by a second, 14 days later. A problem with this method is that there are limitations on the size of tree that can be reached with the sprayer. The maximum tree height using a hydraulic pump sprayer is around 18 meters.

Reardon (1984) and Stipe and Dewey (1985) described the use of systemic insecticides as a means of increasing seed yield. For this technique acephate was implanted or injected into the trees at a time when the vegetative buds were beginning to swell. This treatment resulted in a seed yield increase of 70 to 80 percent over non-treated trees. Because the chemical is placed directly into the vascular system of the tree it is assumed to be relatively safe to the environment.

Silvicultural Control

Before any silvicultural strategy can be devised to combat a pest it is necessary to identify those tree and stand characteristics that are conducive to the population expansion of the insect pest. Once these characteristics are identified it is conceivable that they could be manipulated in such a way as to reduce the vulnerability of

the stand. Blum and MacLean (1984) pointed out, however, that there are other biological and meteorological factors to which the budworm can respond that may override the constraints that silvicultural treatment places upon them. Realizing that other factors influence budworm populations, silviculture can still be a viable tool in combating the budworm.

As mentioned, it is important to first identify the tree and stand characteristics that can promote or hinder budworm activity. The optimal stand for budworm success is described by Williams et al. (1971). This stand is even-aged, has one or more host species and few non-host species, and has much lateral crown exposure with no large openings. Batzer (1969) found no individual tree characteristics that were strongly related to damage, but of nine stand characteristics, three were thought to be related to stand vulnerability; percent basal area of spruce, percent basal area of non-host, and percent basal area of balsam fir. These stand characteristics were related to stand vulnerability as follows: as spruce basal area increased there was a significant increase in balsam fir mortality; increasing basal area of non-host species resulted in a reduction of balsam fir mortality; and increasing the density (trees per unit area) of balsam fir resulted in reduced mortality of that species. Similar conclusions were obtained by Fauss and Pierce (1969) looking at Douglas-fir. They found that stands with less

than 40 percent Douglas-fir suffered less defoliation than did stands with greater than 40 percent.

After identifying stand characteristics that influence the vulnerability, or conversely the susceptibility, of a stand, it is possible to develop a silvicultural strategy that takes those characteristics into account. Westveld (1946) advocated a two phase approach: a hazard reduction phase, and a stand immunity phase. For the first phase "budworm vulnerability maps" are prepared and pre-salvage cutting is conducted in the highly susceptible areas. The second phase consists of species conversion and the maintenance of vigorous growing stock. In building up the stand immunity Prebble and Morris (1951) suggested: (1) developing a mixed species stand with few preferred hosts, (2) managing for short rotations, and (3) promoting fast growing stands on better sites and encouraging non-host species on poor sites.

Jennings et al. (1983) determined that strip clearcuts were effective in reducing the number of first- and second-instar larvae. This reduction was attributed to high mortality resulting from wind, fewer host trees to land on, and increased non-host substrate in the cutover areas. Batzer (1967) looked at the effect of different cutting intensities on subsequent defoliation and found that while partial cutting reduced defoliation slightly, commercial clearcutting reduced it even more. Wulf (1982) maintained that because of the dispersal nature of the larvae even-

aged silvicultural methods should be employed, and that the host overstory be promptly cut following establishment of regeneration in seed tree and shelterwood methods.

Natural Control

Several natural controls operate to help control budworm populations at low densities. Both predators and parasites are important in regulating budworm numbers at endemic levels. Varty (1976) estimated that there are about 150 species of predators and parasitoids of the spruce budworm. Predators consume larvae, pupae, and adults, while parasites generally lay eggs in the hibernating larvae which will eventually develop and kill the host.

When discussing the importance of birds as predators, Mattson (1974) pointed out that both the functional and numerical response must be considered. The functional response is the actual feeding activity of the bird, and the numerical response is the ability of the predator to increase in population. This increase can either be by immigration or by reproductive increases in relation to increasing prey populations. Some birds reach a "consumptive plateau" for larvae at low larval densities and consequently have little effect on higher larval populations unless immigration into the outbreak area occurs.

Predators can exert a big impact on budworm

populations by preying on budworm pupae either in the tree or on the ground. Kelly and Regniere (1985) examined the predation of pupae on the forest floor and found that over 70 percent per day were killed by predators. The most important vertebrate predator was the white-footed mouse, Peromyscus maniculatus (Bangs.). Responsible for an indeterminable amount of predation was an ant, Camponotus herculeanus (L.). A study conducted by Youngs and Campbell (1984) looked exclusively at species of ants that preyed on western spruce budworm pupae. They found nine species in the genus Camponotus and six in the genus Formica. Campbell et al. (1983) investigated the interaction between predaceous birds and ants. Looking at the variation in adult budworm densities they determined that much of the variation was caused by variation in predation on the large larvae and pupae. Surprisingly, they found that at low budworm populations either birds or ants alone caused an equivalent reduction in the number of pupae as was caused by both groups together. At high budworm densities ants had a greater effect on pupae numbers when birds were excluded than the combined affect, possibly due to the birds preying on the ants.

Parasites are also an important regulator of budworm densities. Many species of parasitoids attack budworm larvae. McKnight (1974) listed 28 primary parasitoids of the western spruce budworm in Colorado. Dodge (1961) reported on the parasitism of the budworm larvae by an

ichneumonid, Glypta fumiferana (Vier.), and by Apanteles fumiferana (Vier.), a braconid. Parasitism occurs in the fall by the parasitoid ovipositing an egg into the hibernating larvae, and resumes growth the following spring when the budworm larvae emerges from the hibernaculum. Parasitism as high as 38 percent has been reported (Dodge, 1961). Unfortunately, the larvae are not killed until the fifth or sixth-instar, by which time considerable reduction in the potential cone crop could have occurred.

IMPACT OF THE WESTERN SPRUCE BUDWORM ON BUDS, DEVELOPING CONES AND SEEDS OF DOUGLAS-FIR IN THE INTERMOUNTAIN REGION

The western spruce budworm, Choristoneura occidentalis Freeman (Lepidoptera: Tortricidae), is credited as being the most widely distributed and destructive defoliator in western North America (Carolin and Honing 1972). Much has been written about the defoliation caused by this insect and the resultant damage, including: reduction in height and diameter increment (Silver 1960, Williams 1966, Alfaro et al. 1982 and; Alfaro et al. 1985); volume growth loss (Ferrell and Scharph 1982) and; tree mortality (Alfaro et al. 1982). Another significant impact of Choristoneura spp. is the reduction in the potential seed crop. Schooley (1978) reported on the affect of the spruce budworm, C. fumiferana (Clem.), on cone production by balsam fir, Abies balsamea (L.) Mill. Damage to cones of jack pine, Pinus banksiana Lamb. by the jack-pine budworm, C. pinus Free. is mentioned by Kulman et al. (1963), and Fellin and Shearer (1968) described damage to cones and seeds of western larch, Larix occidentalis Nutt. by the western spruce budworm. Damage to cones of Douglas-fir, Pseudotsuga menziesii var, glauca (Mirb.) Franco. was first described by Dewey (1970). More recently, Chrisman et al. (1983) investigated the impact of defoliation on subsequent cone production, and Fellin et al. (1983) discussed damage to

conelets of Douglas-fir.

Douglas-fir is an economically valuable species, occurring naturally in all of the western states, extending from Mexico to British Columbia. Stehr (1967) found that throughout most of its range Douglas-fir is sympatric with, and a preferred host of, the western spruce budworm. Because of its value Douglas-fir is often the favored species in natural and artificial regeneration of stands where it occurs. Both natural regeneration and planting depend on an adequate supply of seeds which may only become available every 2 to 7 years at lower elevations (Owens 1976), or as infrequent as one in 11 years at high elevations (Lowry 1966).

With the high demand for seed, and the potentially long period between heavy cone crops, it is important to better understand the reduction in the relative quantity of maturing cones and seeds that can be lost as a result of budworm activity. To assess the total impact caused by the western spruce budworm to seed production it is neccessary to quantify the damage at various stages of seed-cone development. Only the direct impact to cone and seed production caused by western spruce budworm feeding is evaluated. No attempt is made to quantify the indirect effect that defoliation has on subsequent cone production.

Methods and Materials

During the winter of 1985 eight stands, ranging from 8

to 15 hectares, were selected on the Boise and Payette National Forests in west-central Idaho. These stands were selected on the basis of: (1) winter and early spring access; (2) homogeneity of the site; and (3) a Douglas-fir component. The stands also had to be far enough apart to allow extrapolation of the results throughout a broad area, but close enough to accomodate intensive sampling over a short period of time. Site and stand data were collected for each location at the time the stands were selected.

A total of 32 Douglas-fir trees (four from each stand) were choosen and permanantly tagged. The candidate trees were selected using several criteria: (1) they could be safely climbed; (2) they were representative of the trees in the stand; and (3) they were physiologically capable of producing cones.

In May each stand was revisited and branch samples collected from the tagged trees. The branch samples consisted of the terminal 25cm of ramdomly selected first-order branches (branch nomenclature follows that of Jensen and Long 1983). The crown was divided into three levels and four quadrants with one sample collected from each quadrant of each level. Many of the crowns were beyond the reach of a pole pruner, thereby requiring the trees be climbed for collection of the branch samples. The 12 branch tips from each tree were separately sealed in plastic bags, the bags then labeled and stored in a snow cache to keep cool. After all of the sample trees were visited the samples were taken

back to the lab where they were refrigerated until examination.

A second collection was conducted in July for maturing cones. The same sample trees that were visited in May were revisited in an effort to obtain cones. Many of the sample trees, however, did not have an adequate number of cones in any one quadrant, making it necessary to gather the cones from the nearest cone-producing tree. Unfortunately, this effectively reduced the number of trees sampled during both periods from 32 to 21. Forty cones were collected from different quadrants of the four sample trees in each stand. The cones from each tree were placed in a paper bag, sealed, and temporarily stored in an ice-chest where they were kept until they could be taken back to the lab for examination.

The final collection was made in September, long after all budworm activity had ceased. Data collected during this last trip was essentially the same as that collected in May. The only difference was that branch tips were collected from only the top two crown levels. This was done because earlier data indicated no significant difference in the amount of defoliation of the combined top two crown levels and that of the entire tree.

In the lab branch samples were examined for amount of defoliation and the number, type, and condition of each bud was noted. Defoliation for each sample was determined by occularly estimating, to the nearest 10%, the amount of

foliage removed from the most current internodes. A branch average was then determined with a method similar to the Fettes' method (Allen et al. 1984), except that a weight proportional to internode length was applied to the defoliation value of each internode. Using the distribution of new foliage (Silver 1962), and the distribution of total foliage (Schmid and Morton 1981), a weighing factor was derived and applied to each crown level, and an estimate of defoliation for the individual trees made.

At the time of the May collection the reproductive buds were beginning to burst. For each sample the number of seed-cone buds and the number of infested seed-cone buds were recorded. A frost during the first week of May, just as the reproductive buds were beginning to burst, resulted in additional seed-cone buds being damaged. This damage was also determined and recorded. From a subsample of 171 branches, all of the pollen-cone buds and seed-cone buds were examined for larvae to determine if larvae were selecting one reproductive bud over another. Crown levels were analyzed separately and a chi-square test used to evaluate differential selection of buds by the larvae.

In the lab 20 cones from each tree were split longitudinally and the number of damaged and undamaged seeds from one face of each cone recorded. An estimate of seed damage for each tree was determined by taking the mean of the 20 cones. This value was considered to be the maximum seed damage by the budworm because at the time the

cones were collected many of the larvae had pupated and some adults were present. A seed viability test would have been valuable in determining the quality of the seeds, but because the cones were collected before they were mature, this information could not be obtained.

The percent of seed-cone buds infested with larvae was determined for each tree. Analysis of variance was then used to test for significant differences between crown levels, and to test for any significant difference in the proportion of seed-cone buds infested between crown levels. The percent of infested seed-cone buds, and the percent defoliation at the end of the season, were used in a regression model to determine correlations between these variables. An analysis of variance was then used to test for differences between stands. If a significant difference between stands was detected, Fisher's least significant difference was used to determine where these differences existed. With the exception of regression analysis, an arc sine transformation of the proportional data was made prior to statistical analysis (Snedecor and Cochran 1980).

The majority of cones exhibited some degree of budworm damage, some was superficial, but most was internal damage. Damage to the cones was rated in an ascending scale of 1 to 5; with 1 indicating no visible damage, 2 and 3 indicating external damage and; 4 and 5 indicating internal damage. In addition to assessing overall cone damage, the percent of seeds destroyed was used in evaluating budworm impact.

Regression models, using the estimated number of seed-cones at the start of the season, percent seed damage, and percent defoliation at the end of the growing season, were used to identify correlations between these parameters. An analysis of variance was used to determine differences in amount of seed damage between trees within stands, and between stands.

Results

Defoliation of current year's foliage was heavy in 1985 with an average tree defoliation of 83%, significantly higher than the 35% average tree defoliation in 1984 ($p < .05$). The average defoliation on a stand basis was also significantly higher in 1985 than in 1984, with significant differences existing between stands only in 1985, (Table 1). Using a model developed by Carolin and Coulter (1972), the increase in defoliation indicates an approximate increase in larval numbers of 300% from 1984 to 1985.

The majority of the seed-cone buds (96.5%) were distributed about equally between the top 2 crown levels, while only 3.5% were found in the lower crown level. A total of 1461 seed-cone buds were examined of which 25% (range 2 to 79%) were infested with the budworm larvae. No significant difference existed in the percentage of infested seed-cone buds between the 3 crown levels. An additional 15% (range 0 to 69%) were destroyed by frost.

From the subsample of 171 branch tips, all of the

seed-cone, pollen-cone, and vegetative buds were examined (Table 2). In all three crown levels the proportion of seed-cone buds infested was significantly higher than the proportion of infested pollen-cone buds. Less than 2% of the vegetative buds contained larvae, but unlike the larvae from the reproductive buds, these larvae were not positively identified as western spruce budworm larvae.

Frozen seed-cone buds, and presumably those infested with larvae, do not develop further but eventually shrivel and fall from the tree. These two factors, therefore, represent a combined reduction of 40% (range 2 to 100%) of the potential cone crop for 1985. This value is considered a conservative estimate because it is not known how many additional seed-cone buds were attacked by larvae after the first collection and before vegetative bud burst. It is unlikely, however, that the value would be much higher because of the large number of cones that matured on many of the trees, and because the population of larvae in expanding buds is presumed to be relatively stable (Carolin and Coulter 1972).

The percent of infested seed-cone buds was not strongly correlated with the amount of defoliation that occurred later in the same season. A simple linear regression model applied to the data indicated that only 2% of the variation in the percent of infested seed-cone buds between trees was explained by the subsequent level of defoliation. Analysis of variance indicated that there was

a significant difference in the percent of infested seed-cone buds between some of the stands (Table 1). Analysis of variance indicated that this difference was not related to elevation or aspect.

Of the 640 cones examined, 76% were or had been infested with larvae, 21% had superficial damage, and only 3% showed no indication of budworm feeding. Even though a large proportion of the cones were infested, dissections of the cones revealed that not all of the seeds were destroyed. Of the 20 cones examined from each tree an average of 57% (range 7 to 100%) of the seeds were destroyed by the budworm. The greatest seed destruction occurred when the larvae severed the vascular system of the cone. When this happened all of the seeds above the point of severence were destroyed.

For each tree the seed damage was plotted against current year's defoliation and the data points fitted with a non-linear function (Fig. 1). This model indicated that 68% of the variation in seed damage between trees could be explained by the percent of current defoliation. The number of predicted cones available to the larvae (initial number of available buds minus the number of destroyed buds) was included as a dependent variable, but resulted in a lower adjusted R^2.

Of the 21 trees that had both seed damage and defoliation damage data, 20 had current year defoliation values greater than 50%. To further support the observation

that seed damage is related to current defoliation, each tree was placed in one of two catogories based on percent defoliation (51 to 75% or 76 to 100%) and the average seed damage for each category determined. The trees in the former category had 40% of the seeds destroyed, significantly less than the 73% of the seeds destroyed of the trees in the latter category.

Discussion

In 1985 the budworm population reached epidemic proportions in each stand examined. The result was that every sample tree experienced a considerable increase in defoliation. The average stand defoliation of current years foliage increased significantly from 1984 to 1985 (mean 197%), but as evident from Table 1, the relative ranking of the stands, with respect to defoliation, did not remain the same. For instance, Hidden Creek had an average tree defoliation of 21% in 1984, which increased to 87% in 1985. Fawn Creek, on the other hand, had average defoliation values of 40% and 79% in 1984 and 1985, respectively. Where as Hidden Creek had lower defoliation in 1984 than did Fawn Creek, the condition was reversed in 1985.

The significance of this change in relative defoliation between stands between years is the implication it presents to anyone attempting to identify site or stand characteristics that may be correlated to defoliation.

Assuming that these characteristics are relatively stable from one year to the next, barring catastrophic events such as fire or logging, one would expect that the relative defoliation between stands would also remain the same from one year to the next. Table 1 indicates, however, that this was not the case between 1984 and 1985.

The combination of warm spring temperatures and early snow melt in 1985 resulted in 25% of the seed-cone buds, and 9% of the pollen-cones buds being infested soon after larval emergence. The significantly greater proportion of infested seed-cone buds could be explained by feeding preference of the larvae, or more likely, because the seed-cone buds are located on the distal part of the shoot and the larvae are photopositive (Thomson 1979), the disproportionate damage to reproductive structures could be incidental. The proportion of infested vegetative buds is included in this report only to indicate that larvae were present in these buds. Because positive identification was impossible, the damage caused by these larvae can not be attributed to the western spruce budworm.

With 25% of the seed-cone buds infested early in the season it is reasonable to expect that a considerable impact could occur to the cone crop during years of low cone production. A study by Fellin et al. (1983) showed that in one case 100% of the conelets were destroyed by the first week of June. Data collected in 1985 indicated, however, that conelet mortality remained relatively low as

demonstrated by the many trees that produced medium cone crops.

Seed-cone bud damage and conelet mortality represents a 100% reduction in seeds from those structures, but as the conelet enlarges the reduction in percent of damaged seeds decreases. It can be seen from Fig. 1 that the percent of damaged seeds per tree is exponentially related to the percent of defoliation per tree. With an average tree defoliation of 83% of the new foliage, and even though 76% of the cones collected were damaged by the budworm, only 57% of the seeds were destroyed. If all of these seeds were viable, considerably more seeds would be available than would be expected from the amount of cone damage. Fig. 1 also illustrates that some trees can have heavy defoliation of current foliage (80 to 90%) and still have only about 50% of the seeds destroyed.

LITERATURE CITED

Alfaro, R. I., G. A. Van Sickle, A. J. Thomson, and E. Wegwitz. 1982. Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. Can. J. For. Res. 12: 780-787.

Alfaro, R. I., A. J. Thomson, and G. A. Van Sickle. 1985. Quantification of Douglas-fir growth losses caused by western spruce budworm defoliation using stem analysis. Ibid. 15: 5-9.

Allen, D. C., L. Dorais, and E. G. Kettela. 1984. Survey and detection, pp. 22-36. In Managing the spruce budworm in eastern North America. U.S. Dep. Agric. For. Serv. Handb. No. 620.

Allen, J. C. 1976. A modified sine wave method for calculating degree days. Environ. Entomol. 5: 388-396.

Arnold, C. Y. 1960. Maximum-minimum temperatures as a basis for computing heat units. Am. Soc. Hortic. Sci. 76: 682-692.

Batzer, H. O. 1960. Mined buds, a hibernation site for spruce budworm. J. Econ. Entomol. 53: 684-685.

1967. Spruce budworm defoliation is reduced most by commercial clearcutting. U.S. Dep. Agric. For. Serv. Res. Note NC-36.

1969. Forest characteristics and vulnerability of balsam fir to spruce budworm in Minnesota. For. Sci. 15: 17-25.

Bean, J. L. 1961. Predicting emergence of second-instar spruce budworm larvae from hibernation under field conditions in Minnesota. Ann. Entomol. Soc. Am. 54: 175-177.

Beckwith, R. C., and D. G. Burnell. 1982. Spring larval dispersal of the western spruce budworm (Lepidoptera: Tortricidae) in north-central Washington. Environ. Entomol. 11: 828-832.

Beckwith, R. C., and W. P. Kemp. 1984. Shoot growth models for Douglas-fir and grand fir. For. Sci. 30: 743-746.

Blais, J. R. 1952. The relationship of the spruce budworm (Choristoneura fumiferana Clem.) to the flowering condition of balsam fir (Abies balsamea (L.) Mill.). Can J. Zool. 30: 1-29.

Blum, B. M., and D. A. MacLean. 1984. Silviculture, forest management, and the spruce budworm, pp. 83-102. In Managing the spruce budworm in eastern North America. U.S. Dep. Agric. For. Serv. Handb. No. 620.

Brubaker, L. B., and S. K. Greene. 1979. Differential effects of Douglas-fir tussock moth and western spruce budworm on radial growth of grand fir and Douglas-fir. Can. J. For. Res. 9: 95-105.

Campbell, R. W., T. R. Torgersen, and N. Srivastava. 1983. A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. For. Sci. 29: 779-790.

Campbell, R. W., N. Srivastava, T. R. Torgersen, and R. C. Beckwith. 1984. Patterns of occurrence of western spruce budworm (Lepidoptera: Tortricidae): larvae, pupae and pupal exuvia, and egg masses. Enviorn. Entomol. 13: 522-530.

Carolin V. M., Jr, and W. K. Coulter. 1972. Sampling populations of western spruce budworm and predicting defoliation on Douglas-fir in eastern Oregon. U.S. Dep. Agric. For. Serv. Res. Pap. PNW-149.

Carolin, V. M., Jr., and F. W. Honing. 1972. Western spruce budworm. U.S. Dep. Agric. For. Serv. Forest Pest Leaflet 53.

1975. Comparison of western spruce budworm populations and damage on grand fir and Douglas-fir trees. U.S. Dep. Agric. For. Serv. Res. Pap. PNW-195.

Carolin, V. M. Jr., and R. E. Stevens. 1979. Key to small lepidopterous larvae in opening buds and new shoots of Douglas-fir and true firs. U.S. Dep. Agric. For. Serv. Res. Note RM-365.

Chrisman, A. B., G. M. Blake, and R. C. Shearer. 1983. Effect of western spruce budworm on Douglas-fir cone production in western Montana. U.S. Dep. Agric. For. Serv. Res. Pap. INT-308.

Cleary, B. D., and R. H. Waring. 1969. Temperature: collection of data and its analysis for the interpretation of plant growth and distribution. Can J. Bot. 47: 167-173.

Dewey, J. E. 1970. Damage to Douglas-fir cones by Choristoneura occidentalis. J. Econ. Entomol. 63: 1804-1806.

Dodge, H. R. 1961. Parasitism of spruce budworm by Glypta and Apanteles at different crown heights in Montana. Can. Entomol. 93: 222-228.

Fauss, D. L., and W. R. Pierce. 1969. Stand conditions and spruce budworm damage in a western Montana forest. J. Forest. 67:322-325.

Fellin, D. G.,and W. C. Schmidt. 1967. Spruce budworm larvae sever stems of western larch shoots in Montana. Ibid. 65: 258-260.

Fellin, D. G., and R. C. Shearer. 1968. Spruce budworm larvae damage western larch cone and seeds. Ibid. 66: 568-570.

Fellin, D. G., and J. E. Dewey. 1982. Western spruce budworm. U.S. Dep. Agric. For. Serv. Handb. No. 53.

Fellin, D. G., R. C. Shearer, and C. E. Carlson. 1983. Western spruce budworm in the Northern Rocky Mountains: biology, ecology, and impacts. West. Wildlands. 9(1): 2-7.

Ferrell, T. G., and R. F. Scharpf. 1982. Stem volume losses in grand firs topkilled by western spruce budworm in Idaho. U. S. Dep. Agric. For. Serv. Res. Pap. PSW-164.

Freeman T. N. 1967. On coniferophagous species of Choristoneura (Lepidoptera: Tortricidae) in North America. Can. Entomol. 99: 449-455.

Furniss. R. L., and V. M. Carolin. 1977. Western Forest Insects. U.S. Dep. Agric. For. Serv. Misc. Publ. No. 1339. 454 pp.

Greenbank, D. O. 1973. The dispersal process of spruce budworm moths. Can. Forest. Serv. Maritimes Forest Research Centre. Fredericton, N. B. Information Report M-X-39.

Harris, J. W. E., A. F. Dawson. 1982. Estimating number of western spruce budworm eggs from egg mass measurements in British Columbia. Can Entomol. 114: 643-645.

Jennings, D. T., M. W. Houseweart, and J. B. Dimond. 1983. Dispersal losses of early-instar spruce budworm (Lepidoptera: Tortricidae) larvae in strip clearcut and dense spruce-fir forests in Maine. Enviorn. Entomol. 12: 1787-1792.

Jennings, D. T., D. G. Fellin, H. O. Batzer, M. W. Housewearth, and R. C. Beckwith. 1984. Techniques for measuring early-larval dispersal of spruce and jack pine budworms. U.S. Dep. Agric. For. Serv. Handb. No. 614.

Jensen, E. C., and J. N. Long. 1983. Crown structure of a codominant Douglas-fir. Can. J. For. Res. 13: 264-269.

Kelly, B., and J. Regniere. 1985. Predation on pupae of the spruce budworm (Lepidoptera: Tortricidae) on the forest floor. Can. Entomol. 117: 33-38.

Kemp, W. P. 1984. Temperature and western spruce budworm development. 1984. A summary prepared for a CANUSA symposium workshop.

Kemp, W. P., and R. C. Beckwith. 1984. A comparison of phenology models developed for western spruce budworm host tree species in northeastern Oregon and north-central Idaho. Unpublished manuscript.

Knight, F. B., and H. J. Heikkenen. 1980. Principles of Forest Entomology. McGraw-Hill, N.Y. 461 pp.

Koslowski, T. T., and C. H. Winget. 1964. The role of reserves in leaves, branches, stems and roots on shoot growth of red pine. Amer. J. Bot. 51: 522-529.

Krueger, K. W. 1967. Nitrogen, phosphorus and carbohydrate in expanding and year-old Douglas-fir shoots. For. Sci. 13: 352-356.

Kucera, D. R., and R. G. Taylor. 1985. Spruce budworm situation in North America. Can. Forest. Serv. Misc. Publ. No. 1436.

Kulman, H. M., and A. C. Hodson. 1961. Feeding and oviposition habits of the jack-pine budworm. J. Econ. Entomol. 54: 1138-1140.

Kulman, H. M., A. C. Hodson, and D. P. Duncan. 1963. Distribution and effects of jack-pine budworm defoliation. For. Sci. 9: 146-157.

Lowry, W. 1966. Apparent meteorological requirements for abundant cone crops in Douglas-fir. For. Sci. 12: 185-192.

MacLean, D. A., and R. G. Lidstone. 1982. Defoliation by spruce budworm: estimation by ocular and shoot-count methods and variability amoung branches, trees, and

stands. Can. J. For. Res. 12: 582-594.

Mattson, W. J. 1974. Negligible feeding responses by birds to variations in abundance of the budworm Choristoneura pinus (Lepidoptera: Tortricidae). Great Lakes Entomol. 7: 104-112.

McDonald, G. I. 1981. Differential defoliation of neighboring Douglas-fir trees by western spruce budworm. U.S. Dep. Agric. For. Serv. Res. Note INT-306.

McKnight, M. E. 1968a. A literature review of the spruce, western, and 2-year cycle budworms. Ibid. RM-44.

1968b. The 24-inch branch as a sample unit for eggmass surveys of the western spruce budworm. U.S. Dep. Agric. For. Serv. Res. Note RM-122.

1969. Distribution of hibernating larvae of the western spruce budworm, Choristoneura occidentalis, on Douglas-fir in Colorado. J. Econ. Entomol. 62: 139-142.

1971. Natural mortality of the western spruce budworm, Choristoneura occidentalis in Colorado. U.S. Dep. Agric. For. Serv. Res. Pap. RM-81.

1974. Parasitoids of the western spruce budworm in Colorado. Enviorn. Entomol. 3: 186-187.

Miller, C. A. 1977. The feeding impacts of spruce budworm on balsam fir. Can. J. For. Res. 7: 76-84.

Montgomery, B. A., J. B. Dimond, J. A. Witter, and G. A. Simmons. 1984. Insecticides for control of the spruce budworm. U.S. Dep. Agric. For. Serv. Handb. No. 615.

Morris, R. F. 1955. The development of sampling techniques for forest insect defoliators, with particular reference to spruce budworm. Can. J. Zool. 33: 325-294.

Morris, R. F., C. A. Miller, D. O. Greenbank, and D. G. Mott. 1958. The population dynamics of the spruce budworm in eastern Canada. Proceedings Tenth International Congress of Entomology. 4: 137-149. Taken from: Thomson, A. J. 1979.

Owens, J. N. 1976. The reproductive cycle of Douglas-fir. Pac. For. Res. Cent. Env. Canada. BC-P-8.

Prebble, M. L., and R. F. Morris. 1951. Forest entomology in relation to silviculture in Canada. Forest. Chron. 27: 6-37.

Reardon, R. C. 1984. How to protect individual trees from western spruce budworm by implants and injections. U.S. Dep. Agric. For. Serv. Handb. No. 625.

Redak, R. A., and R. G. Cates. 1984. Douglas-fir (Pseudotsuga menziesii)-spruce budworm (Choristoneura occidentalis) interactions: the effect of nutrition, chemical defenses, tissue phenology, and tree physical parameters on budworm success. Oecologia. 62: 61-67.

Regniere, J., and R. M. Fletcher. 1983. Direct measurement of spruce budworm (Lepidoptera: Tortricidae) larval dispersal in forest stands. Enviorn. Entomol. 12: 1532-1538.

Schmid, J. M., and M. B. Morton. 1981. Distribution of foliage on open-grown white fir and Douglas-fir in

northern New Mexico, U.S A. Can. J. For. Res. 11: 615-619.

Schmid, J. M., and P. A. Farrar. 1982. Distribution of western spruce budworm egg masses on white fir and Douglas-fir. U.S. Dep. Agric. For. Serv. Res. Pap. RM-241.

Schooley, H. O. 1978. Effects of spruce budworm on cone production by balsam fir. Forest. Chron. 54: 298-301.

Shea, P. G., and P. C. Nigam. 1984. Chemical control, pp. 115-132. In Managing the spruce budworm in Eastern North America. U.S. Dep. Agric. For. Serv. Handb. No. 620.

Silver, G. T. 1960. Notes on a spruce budworm infestation in British Columbia. Forest. Chron. 36: 362-374.

1962. The distribution of Douglas-fir foliage by age. Forest. Chron. 38: 433-438.

Snedecor, G. W., and W. G. Cochran. 1980. Statistical methods, 7th. ed. The Iowa State Univer. Press. Ames, Iowa. 507 pp.

Stage, A. R. 1973. Prognosis model for stand development. U.S. Dep. Agric. For. Serv. Res. Pap. INT-137.

Stark, R. W., and J. H. Borden. 1965. Life history of Choristoneura occidentalis subretiniana Obraztsov (Lepidoptera: Tortricidae) attacking lodgepole pine. Can. Entomol. 97: 684-690.

Stehr, G. W. K. 1967. On coniferophagous species of Choristoneura (Lepidoptera: Tortricidae) in North America. II. Geographic distribution in accordance with

forest regions. Can. Entomol. 99: 456-463.

Stevens, R. E., V. M. Carolin, and G. P. Markin. 1984. Lepidoptera associated with western spruce budworm. U.S. Dep. Agric. For. Serv. Handb. No. 622.

Stipe, L. E. 1984. Ground-spray techniques to reduce damage from western spruce budworm. U.S. Dep. Agric. For. Serv. Handb. No. 624.

Stipe, L. E., J. A. E. Knopf, R. L. Livingston, R. W. Young, and G. P. Markin. 1977. A pilot project with Orthene for control of the western spruce budworm McCall, Idaho 1977. U.S. Dep. Agric. For. Serv.

Stipe, L. E., and J. E. Dewey. 1985. Protecting Douglas-fir cones with a systemic insecticide. U.S. Dep. Agric. For. Serv. Forest Pest Management. Rep. 85-6.

Terrell, T. T. 1959. Sampling populations of overwintering spruce budworm in the Northern Rocky Mountain Region. U.S. Dep. Agric. For. Serv. Res. Note 61.

Thomson, A. J. 1979. Evaluation of key biological relationships of western budworm and its host trees. Can. For. Serv. Pac. For. Res. Cent. Rep. BC-X-186.

Thomson, A. J., and G. A. Van Sickle. 1980. Estimation of tree growth losses caused by pest activity. Can. J. For. Res. 10: 176-182.

Thomson, A. J., and S. M. Moncrieff. 1982. Prediction of bud burst in Douglas-fir by degree-day accumulation. Can. J. For. Res. 12: 448-452.

Thomson, A. J., R. F. Sheperd, J. W. E. Harris, and R. H. Silversides. 1984. Relating weather to outbreaks of western spruce budworm Choristoneura occidentalis (Lepidoptera: Tortricidae) in British Columbia. Can. Entomol. 116: 375-381.

Twardus, D. T., and V. M. Carolin. 1984. How to distinquish between old and new egg masses of the western spruce budworm. U.S. Dep. Agric. For. Serv. Handb. No. 623.

Van Sickle, G. A., R. I. Alfaro, and A. J. Thomson. 1983. Douglas-fir height growth affected by western spruce budworm. Can. J. For. Res. 13: 445-450.

Varty, I. W. 1976. Arthropod predators and parasites, pp. 103-105. In Proceedings of a symposium on spruce budworm. U.S. Dep. Agric. For. Serv. Misc. Pub. 1327.

Volney, W. J. A., W. E. Waters, R. P. Akers, and A. M. Liebhold. 1983. Variation in spring emergence patterns amoung western Choristoneura spp. (Lepidoptera: Tortricidae) populations in southern Oregon. Can. Entomol. 115: 199-209.

Westveld, M. 1946. Forest management as a means of controlling the spruce budworm. J. Forest. 44: 949-953.

Williams, C. B. 1966. Differential effects of the 1944-56 spruce budworm outbreak in eastern Oregon. U.S. Dep. Agric. For. Serv. Res. Pap. PNW-33.

Williams, C. B., P. J. Shea, and G. S. Walton. 1971. Population density of western spruce budworm as related to stand characteristics in the Bitterroot National

Forest. Ibid. PSW-72.

Wulf, N. W. 1982. Management strategies for western spruce budworm (Choristoneura occidentalis Freeman). Unpublished manuscript.

Youngs, L. C., and R. W. Campbell. 1984. Ants preying on pupae of the western spruce budworm, Choristoneura occidentalis (Lepidoptera: Tortricidae), in eastern Oregon and western Montana. Can. Entomol. 116: 1665-1669.

Table 1. Percent defoliation, seed damage, and infested seed-cone buds by stand[a]

Stand name	Defoliation 1984	Defoliation 1985	Seed Damage	Infested Seed-Cone Buds
Lower Road Fk.	61.0a	100.0f	82.0bc	16.0abcde
Sheepweiser	45.0a	89.0cde	52.0a	22.0bcde
Fawn Ck.	40.0a	79.0abcde	41.0a	17.0bcde
Buttergulch	38.0a	100.0f	92.0c	29.0bcde
Death Trap	36.0a	59.0abc	34.0a	14.0abcde
Kennedy Ck.	25.0a	81.0abcde	44.0a	5.0ab
Hidden Ck.	21.0a	87.0bcde	31.0a	43.0ef
Brundage Mt.	14.0a	68.0abcd	82.2b	50.0f

[a] Means followed by the same letters are not significantly different ($P<0.05$; Fisher's least significant difference test).

Table 2. Distribution of bud damage by crown level and by bud type[a]

	No. Buds Examined				% Buds Infested			
	Top	Mid	Bottom	Total	Top	Mid	Bottom	Total
Sample tips	75	63	33	171				
Bud Type								
Seed-cone	425	280	30	735	12.0a	27.1a	40.0a	18.9a
Pollen-cone	5223	4553	1467	11243	7.0b	9.9b	15.6b	9.3b
Vegetative[b]	2840	2396	665	5874	1.2c	2.1c	0.9c	1.6c

[a]Means followed by the same letters are not significantly different ($P<0.05$; Chi-square test).
[b]Larvae found in the vegetative buds were not positively identified as western spruce budworm.

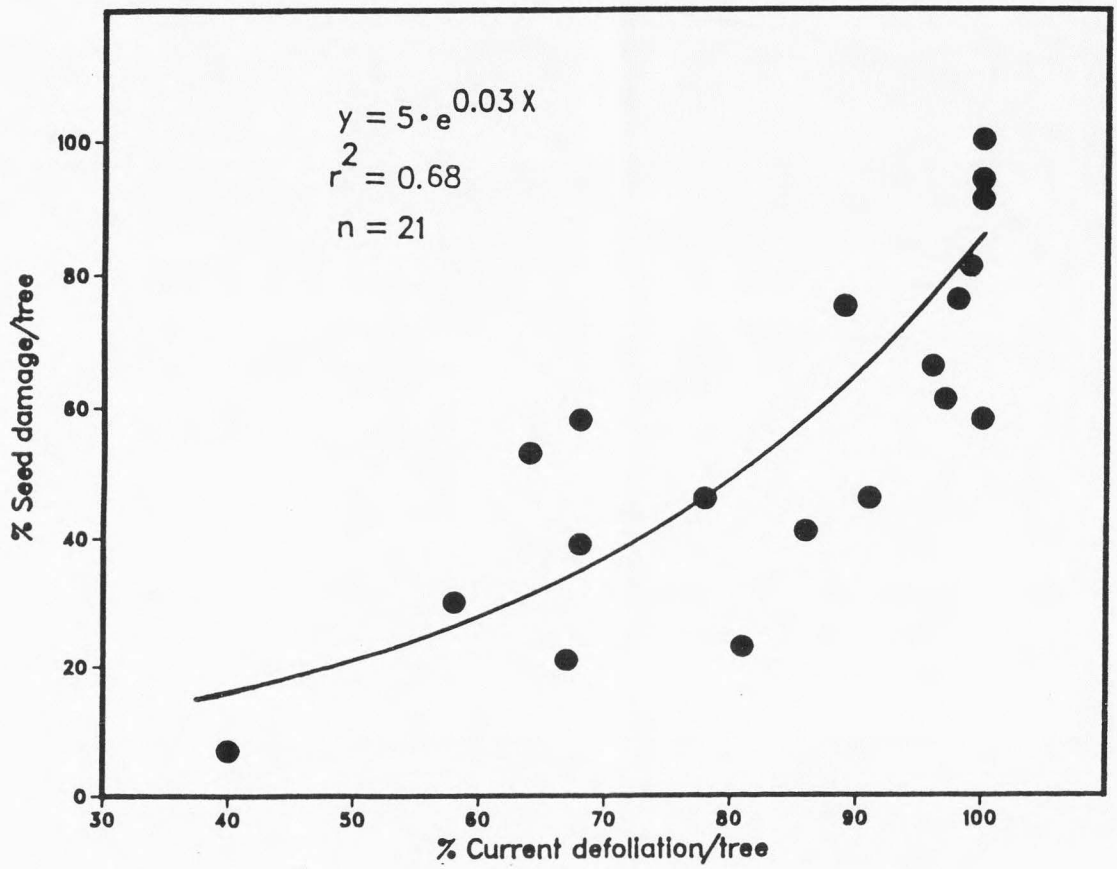

Fig. 1. The relationship between percent of current year's defoliation and percent seed damage